

GENERAL NOTES

Wilson Bull., 98(3), 1986, pp. 459–462

Clutch-size differences in western and introduced eastern populations of House Finches: patterns and hypotheses.—Factors influencing avian clutch size have been discussed by many workers (e.g., Lack 1954, Perrins 1965, Cody 1966, Skutch 1967, Ricklefs 1980, and references therein). Many of these observers have hypothesized that population density, or density relative to food supply can influence clutch size. When population density or population density relative to food supply is low, there should be more food available to raise young, and clutch sizes should be larger.

House Finches (*Carpodacus mexicanus*) are native to western North America from Mexico to British Columbia. An eastern population was established in New York City when cage-bird dealers released House Finches in 1940 (Elliot and Arbib 1953). The released birds probably came from southern California (Elliot and Arbib 1953, Aldrich and Weske 1978). Bock and Lephien (1976), and Bystrak and Robbins (1978) reported that the eastern House Finch population increased exponentially by a factor of 0.24/year during the 1960s through the early 1970s. Here, I examine differences in clutch size in eastern and western House Finch populations and detail how the differences relate to clutch size-specific fledging rates, predation rates, cowbird parasitism rates, and population density. I predicted that clutch size should be greater in the low-density eastern population, which is undergoing exponential growth in a previously unexploited area, because relatively more food would be available to finches there.

Methods.—I used data from the North American Nest Record Card Program (NRCP) conducted by the Cornell University Laboratory of Ornithology. In this program, volunteer observers record location, habitat, and nest history information on standardized cards. Cards are sent to the Cornell Laboratory of Ornithology for editing and computer storage. Peakall (1970) reviewed the NRCP and concluded that this program's clutch-size data are reliable, particularly with large sample sizes, despite the biases inherent in volunteer-based multi-observer programs.

I analyzed only those cards with completed clutches. These included cards with more than one observation of a particular clutch size, an observation of a clutch after the estimated last egg date, or an observation of the number of eggs and young at hatching time. Cards of nests that were deserted during incubation or that were parasitized by Brown-headed Cowbirds (*Molothrus ater*) were not included in clutch size comparisons, but were used in a separate analysis of the possible effects of interspecific competition on clutch size. Additional clutch data were taken from Gill and Lanyon (1965) and Bull (1974). In my analysis of fledging rates, clutch sizes were considered as the largest number of eggs or young reported on a card.

Clutch sizes in the presumed parent southern Californian population (nests inside a block from 33° to 35°40'N by 116° to 119°W) were compared to those in the eastern population (states to the north of North Carolina and east of Indiana). I tested for latitudinal effects by comparing both eastern and northwestern nests at the same latitude (above 36°45'N), and northwestern and southern Californian nests. All comparisons were made using one-tailed *t*-tests with pooled variance (Snedecor and Cochran 1980), as the hypotheses being examined all had a priori predictions. I estimated relative population density in the three areas using Breeding Bird Survey (BBS) data from the U.S. Fish and Wildlife Service. Any difference in density between eastern and western populations could be influenced in part by eastern observers unfamiliar with the introduced House Finches. However, House Finches have

TABLE 1
CLUTCH SIZES AND DENSITIES OF THREE POPULATIONS OF HOUSE FINCHES

	East ^a	West	
		Southern California	Northwest ^b
Density (birds/route) ^c	0.29	42.44	17.20
Mean clutch size	4.53 ± 0.86 (108) ^d	4.21 ± 0.87 (128)	4.35 ± 0.84 (195)

^a Maine, Massachusetts, New Hampshire, Vermont, Ontario, New York, Connecticut, Rhode Island, Pennsylvania, New Jersey, Delaware, Virginia, West Virginia, Kentucky, Ohio, and Michigan.

^b Northern California (>36°45'N), Oregon, and Washington.

^c A route consists of 50 3-min counting locations at 0.8-km intervals.

^d $\bar{x} \pm SD$ (N).

now been in the East for more than 40 years, hence observer recognition is likely, and the BBS rigorously screens the quality of its observers, choosing experienced birders, who are likely to be familiar with House Finches (Robbins and VanVelzen 1967). To determine the influence of clutch size on fledging success, I compared clutch size-specific fledging rates (proportion of eggs fledged) of eastern and western nests using a χ^2 test.

Results and discussion.—Results of NRCP analysis (Table 1) indicate that clutch size is significantly greater in the East than in southern California ($P = 0.002$), despite high variance caused by the discrete nature of clutch size. Several hypotheses might explain this greater clutch size. Clutch size might be greater in the Northeast than in southern California because of latitudinal differences (Lack 1954, Cody 1966, Ricklefs 1980). However, because clutch size in the Northwest was not significantly greater than in southern California ($P = 0.079$), and because it was significantly smaller than in the East ($P = 0.037$) (Table 1), latitude is an unlikely explanation for the difference in clutch size. A second possibility is that clutch size differences result from altitudinal variation (Lack 1954). A comparison of western clutches at different altitudes (<610 m, 610–1220 m, >1220 m), however, showed no significant difference (one-way ANOVA, $P = 0.25$).

A third possibility is that predation pressure or interspecific brood parasitism is higher in the West. First, increased clutch size could make nests easier to detect by predators or brood parasites because of an increased chance of spotting eggs, an increased chance that the young will be heard by a predator, or an increased chance of nest detection if more young require more feeding trips by adults. Several lines of evidence make this hypothesis unlikely. If anything, the proportion of eggs fledging increases overall with increased clutch size in both eastern and western nests (Table 2). Second, cowbird nest parasitism is significantly more common in eastern than in western nests (11 vs 1% of the nests, $P < 0.005$). Finally, cowbirds tended ($N = 46$) to lay in nests well before clutch completion, when clutch sizes were substantially smaller ($\bar{x} = 2.33 \pm 0.91$ [SD]) than completed southern California clutches ($P < 0.005$), suggesting that final clutch size plays little role in nest detection by cowbirds.

A second way predation, as well as catastrophic weather, might affect clutch size is by favoring birds who spread the risk. For example, in an area with a high predation rate, birds that conserve energy by reducing clutch size may be able to lay more eggs later in the nesting season if their first clutch is destroyed. To test this hypothesis, I compared the proportion of nests that failed completely (presumably a reflection of predation or some other extrinsic mortality factor rather than starvation) between the eastern and western finch populations. The proportion of eastern nests that failed completely (no fledged young) was significantly

TABLE 2
PERCENTAGE OF EGGS IN CLUTCHES OF EASTERN AND WESTERN HOUSE FINCHES THAT
FLEDGED

Clutch size	% Total eggs fledged (N)		% Eggs fledged (N) in nests that fledged at least one young	
	East	West	East	West
1	0 (1)	0 (2)	—	—
2	61 (18)	50 (26)	92 (12)	93 (14)
3	68 (123)	59 (144)	90 (93)	89 (96)
4	70 (528)	66 (648)	86 (428)	86 (500)
5	75 (500)	63 (595)	88 (425)	86 (435)
≥6	95 (19)	65 (78)	95 (19)	77 (66)

lower than that of western nests (54 of 286 vs 95 of 357, $P < 0.025$). This supports the spreading-the-risk hypothesis.

The East has a much lower density of House Finches in BBS counts (Table 1) than does the Northwest or southern California, consistent with the density hypothesis. Effects of density on clutch size could be direct, or could interact with food and other resource levels (Lack 1954, Ashmole 1963, Cody 1966, Ricklefs 1980).

After factoring out nests that failed completely, the proportion of eggs that successfully fledged was higher in the eastern population than in the western population for nests with three or more eggs (Table 2). When fledging rates are broken down into clutch size classes greater than and less than the mean clutch size, eastern nests have significantly higher fledging rates in 4-egg nests (binomial test, $P = 0.048$), but not in smaller clutches ($P = 0.37$). In larger clutches, western House Finches produce fewer offspring per energy investment than do eastern individuals (Table 2).

The relative importance of differences in population density and predation rates may be determined if the eastern population reaches equilibrium in the future. If larger clutches in the eastern House Finch result from lower population density, then as the population increases, clutch size should decrease. If the differences in clutch size are the result of differences in predation rates, cowbird parasitism, or other density-independent sources of nest loss, clutch size in the eastern population should remain at its present level.

A third possible explanation for the differences in clutch size is founder effect. This possibility is essentially untestable, although measurements of clutch size heritability might shed some light on its plausibility (Van Noordwijk et al. 1980).

In summary, House Finch clutch sizes are significantly higher in the introduced eastern population than in the native western population. These differences are not explained by differences in latitude or altitude, but may be the result of higher predation rates or population density in the West. Brown-headed Cowbird nest parasitism is higher in the eastern population, but it does not explain differences in clutch size. The difference in cowbird parasitism, which may be caused by a higher density of cowbirds in the East or by a difference in host species availability, merits further investigation. Further examination of clutch size, if the eastern population equilibrates, should shed more light on the relative importance of density and predation on clutch size.

Acknowledgments.—I appreciate constructive criticism and encouragement from C. R. Blem, G. Bucher, T. J. Cade, P. A. Gowaty, J. A. Grzybowski, C. Hall, C. J. Hibbard, N.

T. Wheelwright, and an anonymous reviewer. I would like to thank C. S. Robbins and the staff of the U.S. Fish and Wildlife Service Wildlife Research Laboratory in Laurel, Maryland, for providing the BBS data, and the staff of the Cooperative Research Group of the Cornell Laboratory of Ornithology for helping with NRCP data. Finally, I would like to extend a special thanks to the thousands of volunteer observers who made this study possible. This study was funded in part by an Honors Thesis Grant from the Cornell University College of Agriculture and Life Sciences and an NSF predoctoral fellowship.

LITERATURE CITED

- ALDRICH, J. W. AND J. S. WESKE. 1978. Origin and evolution of the eastern House Finch population. *Auk* 95:528-536.
- ASHMOLE, N. P. 1963. The regulation of numbers of tropical oceanic birds. *Ibis* 103:458-473.
- BOCK, C. E. AND L. W. LEPTHIEN. 1976. Growth in the eastern House Finch population, 1962-1972. *Am. Birds* 30:791-792.
- BULL, J. 1974. *Birds of New York state*. Doubleday, Garden City, New York.
- BYSTRAK, D. AND C. S. ROBBINS. 1978. Bird population trends detected by the Breeding Bird Survey. *Polish Ecological Studies* 3:131-143.
- CODY, M. L. 1966. A general theory of clutch size. *Evolution* 20:174-184.
- ELLIOT, J. J. AND R. S. ARBIB. 1953. Origin and status of the House Finch in the eastern United States. *Auk* 70:31-37.
- GILL, D. E. AND W. E. LANYON. 1965. Establishment, growth and behavior of an extralimital population of House Finches at Huntington, New York. *Bird Banding* 36:1-14.
- LACK, D. 1954. *The natural regulation of animal numbers*. Clarendon Press, Oxford, England.
- PEAKALL, D. B. 1970. The Eastern Bluebird: its breeding season, clutch size and nesting success. *Living Bird* 9:239-253.
- PERRINS, C. M. 1965. Population fluctuations and clutch size in the Great Tit (*Parus major*). *J. Anim. Ecol.* 34:601-647.
- RICKLEFS, R. E. 1980. Geographical variation in clutch size among passerine birds: Ashmole's hypothesis. *Auk* 97:38-49.
- ROBBINS, C. S. AND W. T. VANVELZEN. 1967. The breeding bird survey 1966. U.S. Fish and Wildl. Serv. Spec. Sci. Rept. 102.
- SKUTCH, A. F. 1967. Adaptive limitation of the reproductive rate of birds. *Ibis* 109:579-599.
- SNEDECOR, G. W. AND W. G. COCHRAN. 1980. *Statistical methods*. 7th ed. Iowa State Univ. Press, Ames, Iowa.
- VAN NOORDWIJK, A. J., J. H. VAN BALEN, AND W. SHARLOO. 1980. Heritability of ecologically important traits in the Great Tit. *Ardea* 68:193-203.

J. TIMOTHY WOOTTON, *Dept. Zoology NJ-15, Univ. Washington, Seattle, Washington 98195*.
 Received 5 Aug. 1985, accepted 27 Dec. 1985.